Estuaries Vol. 22, No. 3B, p. 742–752 September 1999

Community Structure and Intertidal Zonation of the Macrobenthos on a Macrotidal, Ultra-Dissipative Sandy Beach: Summer–Winter Comparison

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ABSTRACT: Community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative beach were studied. On the beach of De Panne, Belgium, six transects perpendicular to the waterline (each with five stations) were sampled in September 1995 (summer) and March 1996 (winter). The 30 stations were distributed across the continuum from mean high water spring to mean low water spring in order to sample the macrobenthos at different levels of elevation. The 39 species found had total densities up to 5,500 ind m^{-2} in summer and 1,400 ind m^{-2} in winter. The highest densities were found in the spionid polychaetes *Scolelepis squamata* and *Spio filicornis*, the nephtyid polychaete *Nephtys cirrosa*, the cirolanid isopod *Eurydice pulchra*, and the haustorid amphipods *Bathyporeia* spp. Based on species composition, specific densities, and biomass, two species associations were defined: a relatively species-poor, high intertidal species association, dominated by *S. squamata* and with an average density of 1,413 ind m^{-2} and biomass of 808 mg AFDW m^{-2} (summer); and a relatively species-rich, low intertidal species association, dominated by *N. cirrosa*, and with an average density of 104 ind m^{-2} and biomass of 162 mg AFDW m^{-2} in summer. For both seasons, the high intertidal species association was restricted in its intertidal distribution between the mean tidal and the mean high-water spring level, whereas the low intertidal species association was found from the mean tidal level to the subtidal. The latter showed good affinities with the subtidal *N. cirrosa* species association, occurring just offshore of De Panne beach, confirming the existence of a relationship between the low intertidal and subtidal macrobenthic species associations. Summer–winter comparison revealed a strong decrease in densities and biomass in the high intertidal zone during winter. Habitat continuity of the low intertidal zone with the subtidal allows subtidal organisms to repopulate the low intertidal zone.

Introduction

Although the distribution of macrobenthos on sandy beaches has been well documented in many parts of the world (e.g., Morton and Miller 1968; Trevallion et al. 1970; McLachlan et al. 1981; Dexter 1983; Straughan 1983; Ismail 1990; McLachlan 1990; Jaramillo et al. 1993; Rakocinski et al. 1993; Souza and Gianuca 1995), the macrobenthos inhabiting European and particularly Belgian sandy beaches has been poorly studied (Elliott et al. 1996). Moreover, many still consider these sandy beaches 'biological deserts,' justifying biologically the malification of beaches for coastal protection works and tourism developments. However, the beaches along the 65-km-long Belgian coastline provide food resources for a rich avifauna and marine fauna. The avifauna, consisting of waders such as sanderling, *Calidris alba* use food resources of the beaches in winter (Devos et al. 1996). At high tide a rich marine fauna enters the intertidal zone (e.g., smaller fish such as juvenile plaice [*Pleuronectes platessa*]) (Beyst unpublished information). The food of these birds and fishes consists mainly of the macrobenthos inhabiting the intertidal zone (e.g., Witherby et al. 1947; Thijssen et al. 1974), underscoring the ecological importance of Belgian sandy beaches.

As expected for a macrotidal, ultra-dissipative beach, such as the beach of De Panne (Jaramillo et al. 1993), Elliott et al. (1996) found indications of the presence of a rich intertidal macrobenthic fauna with a maximum density of 600 ind m^{-2} just

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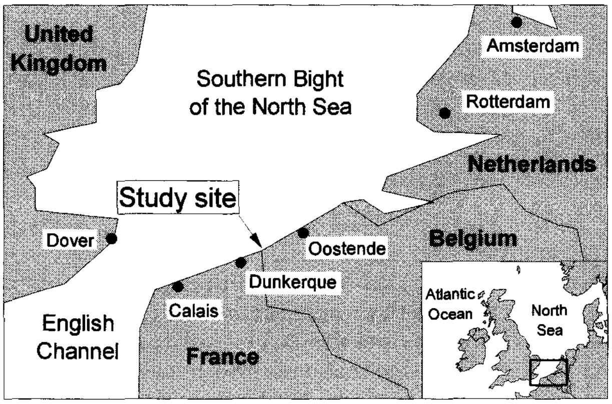

Fig. 1. Geographical disposition of the study area.

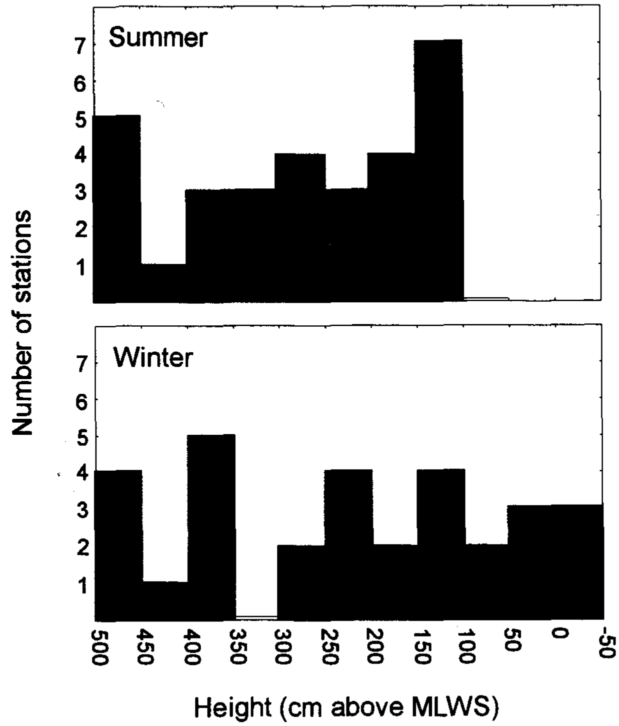

Fig. 2. The distribution of the 30 stations along the intertidal continuum during the summer and winter sampling campaign.

above the mean tidal level, decreasing up and down the beach to a minimum of 100 ind m^{-2}. As the pilot study by Elliott et al. (1996) was based on only one transect and one sampling date, a larger benthic survey is necessary to obtain a more comprehensive view on the zonation of the macrobenthos of this macrotidal, ultra-dissipative beach.

The object of this study was to describe community structure and the pattern of intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative beach in summer and winter.

Material and Methods

Study Area

A 4-km-long beach fronting the Westhoek dune reserve (51°05′12″N to 51°07′00″N and 2°31′06″E to 2°34′00″E) was selected for this study; the reserve extends from De Panne (Belgium) to Bray-Dunes (France) (Fig. 1). The beach habitat is located in a cold-temperate region: air temperatures ranged between 10°C and 25°C in September 1996 and between 5°C and 13°C in March 1997; seawater temperature was 18°C in September 1996 and 8°C in March 1997. During winter 1996–1997, the minimum air temperature was −15°C, whereas the minimum seawater temperature was 2°C (Department of Waterways and Coast unpublished data).

The width of the intertidal zone is approximately 450 m, increasing in width toward the French section. Mean spring and neap tide ranges are 5 m and 3 m, respectively, modal breaker height is 0.5 m and modal wave period is 3 s (Department of Waterways and Coast unpublished data). The general slope of the beach is ca. 1:90 (Lahousse unpublished information), decreasing toward the French section. Sediments are composed of fine sands (median grain size < 250 μm). The beach has several shallow troughs and bars, parallel to the water's edge with an average period of several tens of meters, in which water is retained on the outgoing tide.

Although there are some housing developments and a campsite within a small section of the foredune zone, the relatively small number of visitors to the beach (because of restricted access) and the lack of groins makes this site relatively unimpacted compared to other Belgian beaches. At one transect, situated within the Belgian section of the beach, the landward margin of the intertidal zone is interrupted by a small concrete stormwater dike between the mean high-water neap (MHWN) and mean high water spring (MHWS) level. At the other three transects in the Belgian section this stormwater dike is located above the MHWS level. The French section, which has two transects, has a natural beach-dune transition.

Sampling Strategy

Six transects equally spaced along the beach and oriented perpendicular to the waterline were sampled. Each transect had five stations; two replicate samples were taken per station. The 30 stations were distributed across the continuum from the mean high-water spring level to mean low-water spring level in order to sample the macrobenthos at different elevations on the beach (Fig. 2). In September 1995 (summer) the stations were divided between the MHWS and mean low-water spring (MLWS) levels; in March 1996 (winter) between MHWS and MLWN. In summer, all stations were located between 500 cm and 100 cm above MLWS, whereas in winter, samples were taken between 500 cm and −50 cm above MLWS. The use of six transects equally spaced along the beach allowed generalization of the results to the whole beach, which cannot be represented adequately by just one transect (Haynes and Quinn 1995).

Following Elliott et al. (1996), samples were taken by excavating sediment enclosed by a frame, with a surface area of 0.1026 m^2, to a depth of ca. 0.15 m. Organisms were retained on a 1-mm sieve, fixed and preserved in an 8% formaldehyde-seawater solution. An additional core (3.6 cm diameter, penetration depth of 0.15 cm) was collected with each macrofauna sample for the analysis of sediment characteristics. Height above MLWS at each sampling site was determined from data provided by the Department of Waterways and Coast.

Although the sampling technique is frequently used in the study of intertidal macrofauna, depending on the beach type, different surface areas, excavating depths, number of stations, and number of replicates are used (e.g., McIntyre and Eleftheriou 1968; McDermott 1987; McLachlan 1990; Jaramillo et al. 1993; Haynes and Quinn 1995; Souza and Gianuca 1995). The pilot study of Elliott et al. (1996) revealed that densities of dominant species of the beach in De Panne were high enough that a sampling surface of about 0.1 m^2, an excavation depth of 15 cm, and two replicates per station, would satisfactorally represent the macrobenthic zonation of Belgian beaches. The lugworm *Arenicola marina* occurred in the study area, mainly in the troughs and toward the lower beach, but was not sampled quantitatively by this sampling technique and was not included in analyses.

As the percentage of species expected increases with an increase in total sampling area, the total sampling area needs to be large enough to attain a representative sample of the macrobenthos of the beach. For the dissipative beaches, with a high diversity (Jaramillo and McLachlan 1993), a sampling area of at least 4 m^2 is advised (Jaramillo et al. 1995). The total sampling area in this study was 6 m^2 in both seasons and should thus be sufficient enough to collect more than 95% of the total number of species present on the beach.

The beach of De Panne consists of a series of bars and troughs, each with different habitat characteristics (e.g., the retention of water in the troughs might harbor subtidal fauna, Dörjes 1976). As all samples were taken on top of the bars, this study excluded the macrobenthos of the troughs. In addition, to avoid bias due to tidal vertical migration of hyperbenthic organisms, samples were always taken on exposed sediments, just above the waterline. Thus, sampling always started at high tide and followed the receding water down the beach, ending at the low tidal level.

Laboratory Methods

In the laboratory, the sediment collected for faunal analysis was elutriated 10 times to separate most of the fauna from the sediment. The remaining material was then examined using a dissecting microscope to collect the larger macrobenthic fauna, such as bivalves, that were too heavy to be floated out by elutriation. Macrobenthic organisms were removed, identified to species if possible and counted. Biomass (ash-free dry weight, or AFDW) estimates of all polychaetes, except for the Nephtyidae, and crabs were obtained by loss of mass on ignition (500 ± 50°C for 2 h) of oven-dried samples (70°C for 48 h). The biomass of all other fauna was calculated by regression analysis (Govaere 1978; Mees 1994; Degraer and Vincx 1995).

Sediment samples were oven-dried at 105°C for 12 h, and then ashed at 500 ± 50°C for 2 h to determine total organic matter (TOM) by loss of mass on ignition. The gravel fraction (mainly shell fragments) was that proportion by mass of sediment with a grain size larger than 850 μm. The grain size distribution of the particles smaller than 850 μm was determined with a Coulter LS. The percentage by mass of sand CO_3^{2-} content was determined by measuring the volume of CO_2 released from oven-dried sand upon addition of 25% HCl.

Mathematical Analyses

The morphodynamic state of the beach is given by Dean's parameter ($\Omega = H_b/w_s T$) and the relative tidal range ($RTR = MSR/H_b$), where H_b is the modal breaker height in meters, w_s is the sediment fall velocity in m s^{-1}, T is the modal wave period in s, and MSR is the mean spring tide range in meters (Masselink and Short 1993). Sediment fall velocity is estimated from the median grain size (Anonymous 1995).

Macrobenthic abundances (no. m^{-2}) were used to calculate the diversity as the number of species per sample (N_0) (Hill 1973), the Shannon-Wiener diversity index (H') (Shannon and Weaver 1949), and the Simpson dominance index (SI), each after $\log_{10}$ transformation. To investigate the vertical distribution patterns (from high to low water zonation), the macrobenthic density data were subjected to three multivariate techniques: TWINSPAN, Canonical Correspondence Analysis, and Cluster Analysis. TWINSPAN (Two-Way INdicator SPecies ANalysis) is a Fortran program for arranging mul-

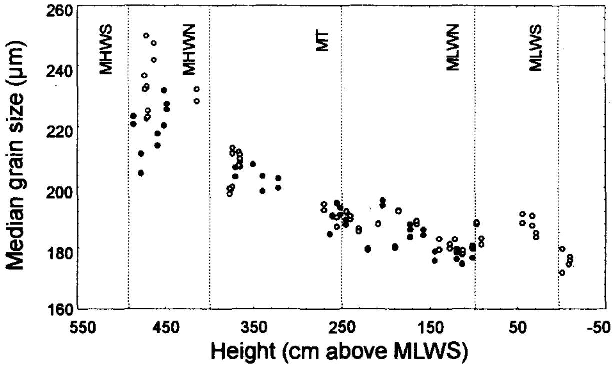

Fig. 3. The intertidal distribution (height in cm above MLWS) of the median grain size (µm). ●: summer; ○: winter.

tivariate data in an ordered two-way table by classification of the individuals and attributes (Hill 1979). After the density was normalized by means of a fourth-root transformation (Sokal and Rohlf 1981; Field et al. 1982), the data were further subjected to a (Canonical) Correspondence Analysis (CA and CCA) (Ter Braak 1988), which included elevation and sand physical and chemical properties as environmental variables. Cluster Analysis of the data used the Bray-Curtis similarity index and the group averaging (Clifford and Stephenson 1975).

The polynomial functions, showing the general zonation trend of the total abundances, the biomass, the number of species per station, and the densities of *Scolelepis squamata, Spio filicornis, Nephtys cirrosa, Eurydice pulchra, Bathyporeia* spp., and *Urothoe poseidonis,* were developed by means of a distance-weighted, least-squares smoothing procedure within the program STATISTICA. Correlations between the environmental variables were analyzed by means of the nonparametric Spearman rank correlation coefficient (Siegel 1952; Conover 1971).

Results

Physical Environment

All intertidal sediments at De Panne beach (between −10 cm and 500 cm above MLWS) consisted of fine, well-sorted sands. A general trend of increasing median grain sizes (from 170 µm to 250 µm) with increasing height on the beach was found in both summer and winter (Fig. 3), and no obvious differences in the sedimentology of summer and winter could be detected. Between 4 m and 5 m height a slightly coarser sediment appeared in winter. The percentage of CO_3^{2-} in the sediment varied between 7% and 32% and averaged about 16%. The TOM was found to be low, between 0.42% and 1.4%, with an average of 0.63%. For both seasons, height on the beach was related ($p < 0.001$) with modal grain size, sorting, and skewness. The percentages of CO_3^{2-} and TOM were correlated with the height on the beach during one season only (CO_3^{2-}: $p < 0.003$, winter; TOM: $p < 0.001$, summer).

With an average median grain size of 221 µm (summer) and 230 µm (winter) of the uppermost beach stations, H_b of 0.5 m and T of 3 s, Dean's parameter (Ω) was estimated at 6.9 in summer and 6.6 in winter. For both seasons, the estimated relative tidal range (RTR) was 10. The beach type can be considered as being ultra-dissipative (Masselink and Short 1993).

Macrobenthos

On the beach of De Panne–Bray-Dunes, a total of 39 macrobenthic species were found (28 in summer and 32 in winter), of which 15 were polychaetes, 7 amphipods, and 6 bivalves. Polychaetes generally exhibited the highest densities and biomass (Fig. 4a,b). Isopods (summer) and amphipods (both seasons) were numerically abundant, while all other taxa—namely, ostracods, copepods, cumaceans, mysids, decapods, and bivalves—were represented by low densities and biomass. The average number of species per sample (N_0) (3–4) was similar in summer and winter (Fig. 4c). The average Shannon-Wiener diversity index (H′) was 0.7 (summer) and 1.3 (winter), whereas the average Simpson dominance index (SI) was 0.5 and 0.6, in winter and summer, respectively.

Of the 39 species only five were present in high densities (at least 25 specimens over all the samples in both seasons), namely the spionid polychaetes *Scolelepis squamata* and *Spio filicornis,* the nephtyid polychaete *Nephtys cirrosa,* the cirolanid isopod *Eurydice pulchra,* and the haustorid amphipods *Bathyporeia* spp. In summer, *S. squamata* and *E. pulchra* each accounted for 30% of the average macrobenthic density of 725 ind m^{-2} (Table 1) over the full intertidal gradient. In winter, lower numbers generally were found, with an average macrobenthic density of 250 ind m^{-2} and dominance by *S. squamata* (30%). In summer, spionid polychaetes accounted for 80% of a macrobenthic biomass of 470 mg AFDW m^{-2}, while in winter this percentage was lower, but still 45% of 473 mg AFDW m^{-2}. The only other species with a considerable biomass, *N. cirrosa,* represented about 15% of the macrobenthic biomass in both seasons.

In summer, the maximum macrobenthic density (5,500 ind m^{-2}) was located at mean tidal (MT) level, showed a sharp decline to MHWS and MLWN levels and increased toward the MLWS level (Fig. 5a). In winter, the maximum density (1,400 m^{-2}) was found at about MHWN, and decreased

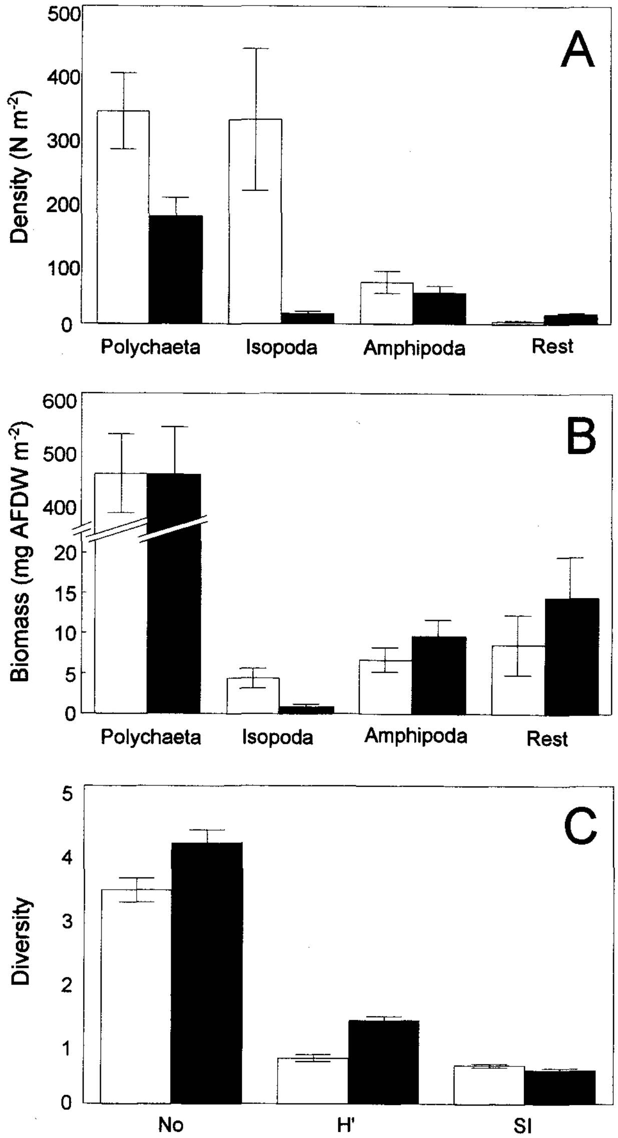

Fig. 4. The distribution over the different taxa of A) the density (no. m^{-2} ± standard error, SE) and B) the biomass (mg AFDW m^{-2} ± SE). C) Diversity indices (number of species per sample, N_0, and Shannon-Wiener diversity index, H′, both ± SE) and evenness index (Simpson dominance index, SI, ± SE). Summer: white bars; winter: black bars.

toward the MHWS and MT levels. The minimum density was located at MHWS, followed by MLWN levels. From the MLWN level on down the beach the macrobenthic density increased slightly. The macrobenthic biomass followed the same trend as the macrobenthic density, with a maximum of about 2,000 mg AFDW m^{-2} in both seasons around MHWN or MT (Fig. 5b). The number of species per sample was highly variable but reached its maximum (seven species for both seasons) at the MT level (Fig. 5c).

Multivariate analyses (TWINSPAN, (C)CA, and Cluster Analysis) revealed two groups (species associations), differentiated by their intertidal distribution: a high intertidal and a low intertidal species association. The transition between the low and high intertidal species associations was approximately 250 cm above MLWS in summer (Fig. 6a), whereas in winter it was approximately 200 cm above MLWS (Fig. 6b). In both seasons, macrobenthic density and biomass were greater in the high intertidal species association: averages of 1,413 ind m^{-2} and 808 mg AFDW m^{-2} in the high intertidal and averages of 162 ind m^{-2} and 407 mg AFDW m^{-2} in the low intertidal species association (Table 2). For N_0 (3–4 species) no differences between species associations or periods were detected. For both seasons, the total number of species per species association was higher in the low intertidal species association, with a maximum of 22 species in March. Of the top five species per species association, the three most abundant species remained the same over time, with only a minor shift in dominance. These species were *Nephtys cirrosa, Spio filicornis,* and *Urothoe poseidonis* for the low intertidal species association and *Scolelepis squamata, Eurydice pulchra,* and *Bathyporeia* spp. for the high intertidal species association. *Spio filicornis, N. cirrosa,* and *U. poseidonis* were generally found from about the MT level on down the beach, increasing in density toward the subtidal (only in winter for *S. filicornis*) (Figs. 7b,c, and f). In summer, S. *squamata, E. pulchra,* and *Bathyporeia* spp. occurred between the MT and MHWS levels and each had maximum density just below MHWN (Figs. 7a,d,

TABLE 1. Average densities and biomass (± standard error, SE) of all species with at least 25 specimens in both sampling periods. P, Polychaeta; I, Isopoda; A, Amphipoda.

	Density (no. m^{-2} ± SE)		Biomass (mg AFDW m^{-2} ± SE)	
	Summer	Winter	Summer	Winter
Scolelepis squamata (P)	287 ± 62	107 ± 31	377 ± 78	212 ± 67
Spio filicornis (P)	4 ± 2	10 ± 3		
Nephtys cirrosa (P)	37 ± 6	38 ± 6	61 ± 11	74 ± 14
Eurydice pulchra (I)	301 ± 107	15 ± 3	4 ± 1	0.9 ± 0.3
Bathyporeia spp. (A)	63 ± 17	34 ± 9	6 ± 1	4 ± 1
All species	725 ± 162	250 ± 33	470 ± 76	473 ± 88

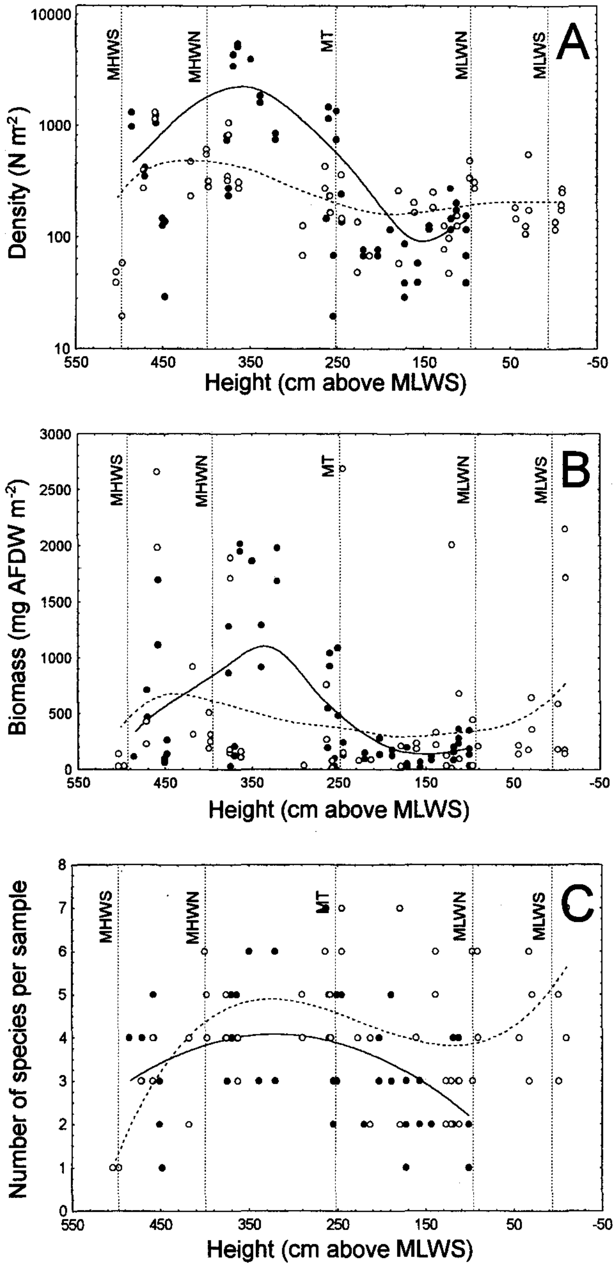

Fig. 5. The intertidal distribution (cm above MLWS) of the macrobenthic density (no. m^{-2}), macrobenthic biomass (mg AFDW m^{-2}), and number of species per sample. ●: summer; ○: winter; density presented on a logarithmic scale.

and e). In winter, the highest densities of *S. squamata* were between the MHWN and the MHWS levels and *E. pulchra* was distributed throughout the intertidal zone.

Discussion

Species Composition and Abundance

The world-wide dominance of polychaetes, crustaceans, and bivalves on sandy beaches (e.g., Dexter 1983; McLachlan 1983; Junoy and Viéitez 1992) is obvious on the ultra-dissipative beach of De Panne. Polychaetes dominate in terms of density (*Scolelepis squamata*), biomass (*S. squamata* and *Nephtys cirrosa*), and number of species; crustaceans are numerically abundant (*Eurydice pulchra*) and are relatively speciose (e.g., amphipods: seven species); and although bivalves are represented in low numbers, six bivalve species were encountered.

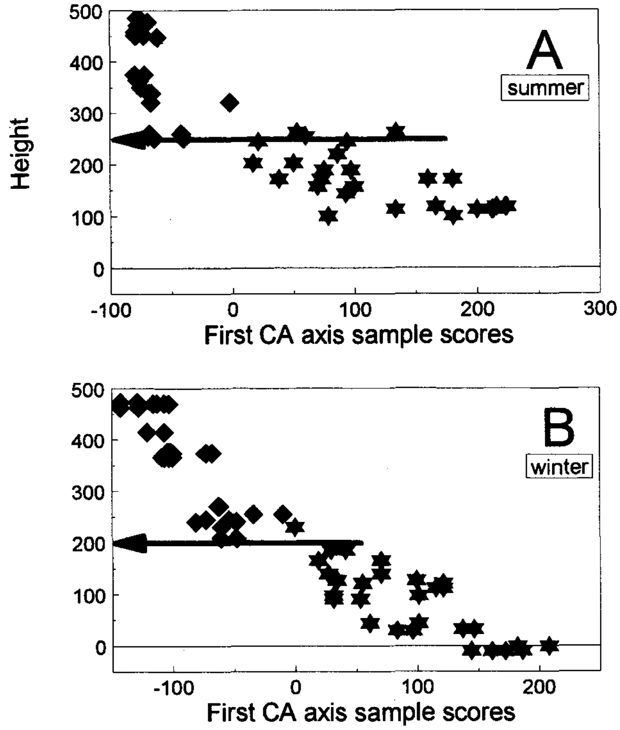

Fig. 6. The continuous relation between the CA sample scores of the first axis and the height on the beach (cm above MLWS); with indication of the two species associations (★: species association 1 and ♦: species association 2) and the distinctive height between both (arrow). The sample scores on the first CA axis explained 31.1% of a total percentage of variance within the species data of 66.1% explained by the first four axes in summer and 18.9% of a total of 44.4% in winter.

The polychaetes *S. squamata, Spio filicornis,* and *N. cirrosa,* the isopod *E. pulchra,* and the amphipods *Bathyporeia* spp. are abundant on various European beaches (e.g., Stephen 1929; Elmhirst 1931; McIntyre and Eleftheriou 1968; Dörjes 1976; Junoy and Viéitez 1992). *Scolelepis squamata* is also abundant on several beaches outside Europe (e.g., Brazilia: Souza and Gianuca 1995; Florida: Rakocinski et al. 1993; New Jersey: McDermott 1987).

As expected from the general trend of an increasing number of species from the reflective toward the dissipative beach type (Jaramillo and McLachlan 1993), more species (39 species) were found on the ultra-dissipative beach of De Panne in comparison to other ultra-dissipative beaches

TABLE 2. Summary table of the general characteristics (± standard error, SE) of the two species associations in summer and winter; with density as no. m^{-2} and biomass as mg AFDW m^{-2}. P, Polychaeta; I, Isopoda; A, Amphipoda.

Intertidal Distribution	Species Association 1 Low Intertidal Zone MLWS—MT		Species Association 2 High Intertidal Zone MT—MHWS	
	Summer	Winter	Summer	Winter
Density	104 ± 11	162 ± 19	1,413 ± 293	332 ± 58
Biomass	162 ± 21	407 ± 105	808 ± 132	534 ± 141
Number of species per sample	3 ± 1	4 ± 1	4 ± 1	4 ± 1
Total number of species	13	22	10	16
The five most dominant species	*Nephtys cirrosa* (P) *Spio filicornis* (P) *Scolelepis squamata* (P) *Urothoe poseidonis* (A) *Bathyporeia* spp. (A)	*Nephtys cirrosa* (P) *Urothoe poseidonis* (A) *Spio filicornis* (P) *Eurydice pulchra* (I) *Magelona papillicornis* (P)	*Eurydice pulchra* (I) *Scolelepis squamata* (P) *Bathyporeia* spp. (A) *Eurydice affinis* (I) *Eteone longa* (P)	*Scolelepis squamata* (P) *Bathyporeia* spp. (A) *Eurydice pulchra* (I) Ostracoda *Eteone longa* (P)

(e.g., 14 species: Jaramillo et al. 1993; 35 species: Souza and Gianuca 1995; 15 species: James and Fairweather 1996). If all habitats of the beach of De Panne (subterrestrial fringe, above MHWS, and intertidal troughs) would have been taken into account it is likely even more species would be found.

As most studies do not provide information on average densities or biomass or use other standardizations (expressed per meter of shoreline), comparison with other studies is very difficult. Yet, it appears that the average density (summer: 725 ind m^{-2}; winter: 250 ind m^{-2}) is high (Haynes and Quinn 1995; Souza and Gianuca 1995), as expected for an ultra-dissipative beach (Jaramillo et al. 1993; McLachlan and Jaramillo 1995; McLachlan et al. 1996).

Macrobenthic Zonation

In this study, two major restrictions on the zonation pattern have to be taken into account: the absence of samples in the subterrestrial fringe (just above MHWS) (Dahl 1952), and the absence of samples in the troughs of the intertidal zone. Both zones may harbor other macrobenthic organisms, representing new species associations, which could not be detected in this study. The description of the zonation is still preliminary and should be interpreted with caution. The existence of at least two intertidal species associations is demonstrated: between the MHWS and MT level (Dahl's [1952] midlittoral zone) a species association dominated by *Scolelepis squamata* and, in summer also by *Eurydice pulchra,* occurs, and between the MT and MLWS level (Dahl's [1952] sublittoral fringe) the species association is dominated by *Nephtys cirrosa.* At about MT level an overlap of the two species associations exists. The high intertidal species association has a low number of species (summer: 10 species; winter: 16 species), occurring at high densities (summer: 1,413 ind m^{-2}; winter: 332 ind m^{-2}), whereas the low intertidal species association is composed of more species (summer: 13 species; winter: 22 species) but at lower densities (summer 104 ind m^{-2}; winter: 162 ind m^{-2}). The biomass followed the same trend as the density, with the highest values (maximum 808 mg AFDW m^{-2}) in the high intertidal zone. A general increase in the number of species, together with a general decrease of the densities, from the high intertidal toward the low intertidal, is a typical characteristic for many sandy beaches world-wide (e.g., Souza and Gianuca 1995).

A detailed review of macrobenthic zonation on sandy beaches is given by McLachlan and Jaramillo (1995): concerning the strictly intertidal zone (between MHWS and MLWS), generally two macro-

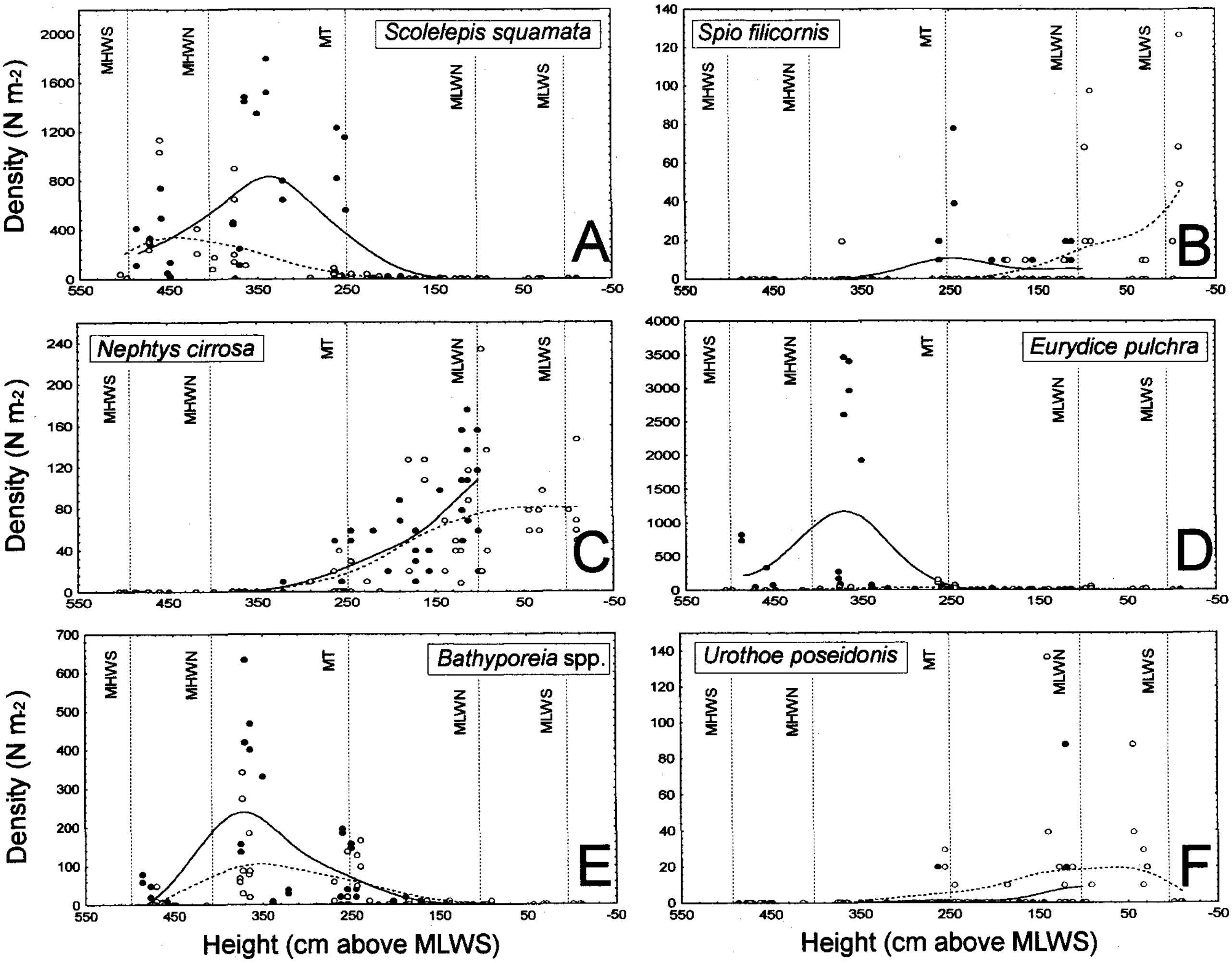

Fig. 7. The intertidal density (no. m^{-2}) distribution of the three most dominant species of each species association and per sampling campaign: A) *Scolelepis squamata*; B) *Spio filicornis*; C) *Nephtys cirrosa*; D) *Eurydice pulchra*; E) *Bathyporeia* spp.; F) *Urothoe poseidonis*. ●: summer; ○: winter.

benthic zones can be distinguished, and the low intertidal zone tends to split into two macrobenthic zones on dissipative beaches. In their pilot study, Elliott et al. (1996) reported the existence of three species associations between MHWS and MLWS on the beach of De Panne: an uppermost species association, dominated by *Bathyporeia* spp.; a high intertidal association, dominated by *S. squamata*; and a low intertidal zone, dominated by *N. cirrosa*. At the natural existence of the uppermost species association, dominated by *Bathyoreia* spp., is doubtful because of the presence of a stormwater dike between MHWS and MHWN. In this study, where only the uppermost intertidal of the first transect was restricted by a stormwater dike, *Bathyporeia* spp. and *S. squamata* were found between 200 cm and 500 cm above MLWS. The population optimum of *Bathyporeia* spp. was only little higher than the optimum height for *S. squamata* (370 cm above MLWS versus 350 cm above MLWS). The expected division of the low intertidal species association on a macrotidal, ultra-dissipative beach (McLachlan and Jaramillo 1995; Souza and Gianuca 1995; Borzone et al. 1996; McLachlan et al. 1996) was not apparent in this study. The troughs on the beach, which were not taken into account in this study, may harbor other species associations not detected in this study.

The vertical distributions of several species of the low intertidal species association (e.g., *N. cirrosa* and *Spio filicornis*) are restricted to the zone below the MT level and these species seem to reach their optimum at or below MLWS. Comparison of the five most dominant species of this low intertidal species association with the dominant species of the subtidal *N. cirrosa* species association (as described by Degraer et al. in press) reveals that *N. cirrosa* is always present in high numbers and four species (the polychaetes *N. cirrosa* and *Magelona papillicornis* and the amphipods *Urothoe poseidonis* and *Bathyporeia* spp.) are abundant in both species associations. Only three of the dominant species of the subtidal *N. cirrosa* community (*Ensis* spp., *Eumida sanguinea,* and *Diastylis bradyi*) were absent in the intertidal zone. Except for *U. poseidonis,* the most dominant species had lower densities in the low intertidal zone in comparison with the subtidal zone.

In comparison with the subtidal macrobenthos (more than 70 species, Degraer et al. In press), the intertidal zone comprises only 39 species. Although temporal variations have to be considered, these findings suggest the low intertidal species association is an intertidal extension of the subtidal *N. cirrosa* species association. The relation between intertidal and subtidal macrobenthic species associations has been demonstrated by other authors (e.g., McIntyre and Eleftheriou 1968; Souza and Gianuca 1995; Borzone et al. 1996). The stress of longer exposure time, positively correlated with the height on the beach, creates a suboptimal situation for the originally subtidal populations and causes a decrease in density, biomass, and number of species higher on the beach. At the MT level (exposed for 6 h twice daily) no subtidal organism is likely to survive. Samples were taken at lower levels on the beach in winter and thus in the optimal habitat for these low intertidal species, which explains the higher average density and biomass of the low intertidal species association in winter in comparison to summer, the higher number of species found in winter (22 species) in the low intertidal zone in comparison to summer (13 species), and the presence of new, typically subtidal species (the polychaetes *Sigalion mathildae, Spiophanes bombyx, Anaitides mucosa, M. papillicornis,* and *Harmothoe* sp. and the bivalve *Tellina tenuis,* Degraer et al. in press) in winter. Critical evaluation of the intertidal distribution of the samples when comparing low intertidal species association characteristics with other studies is advised.

Summer–Winter Comparison

Temporal changes within the macrobenthos of sandy beaches may be related to changes in density and biomass of different species, caused by recruitment, mortality, and production (e.g., Ismail 1990; Bamber 1993; Santos 1994; Souza and Gianuca 1995; Jaramillo et al. 1996). As the temporal variation in this study is based on one summer (September 1996) and one winter campaign (March 1997), the observed temporal variation cannot be attributed to seasonality alone.

Whereas the macrobenthic density and biomass of the low intertidal species association remained more or less constant during the sampling period, a decrease between summer and winter was obvious for the high intertidal species association. The drastic decrease of the density and biomass in the high intertidal zone may be explained by the heavy storms, which affected the sediment in the uppermost stations (slightly increasing the coarseness), and the freezing temperatures, covering the high intertidal zone with ice (personal observation), prior to the winter sampling campaign. In the low intertidal zone, no impact of the storm on the sedimentology was observed, and because of the more frequent submergence of the low intertidal zone, temperatures on and in the sandy sediments were buffered by the more temperate water (minimum 2°C). On the other hand, even with high mortality rates during winter, the low intertidal species association can retain similar densities and biomass due to a possible continuous influx of animals from the subtidal into the low intertidal zone. The high intertidal species association lacks this habitat continuity with a source of immigrants: strong disturbances may deplete these populations.

It can be concluded that the macrobenthos of the macrotidal, ultra-dissipative sandy beach of De Panne is similar to that of other beaches worldwide. Even though all beach habitats have not been taken into account, the number of species recorded in this study exceeds the number of species found on most other beaches. Two species associations, correlated with elevation, were detected. The low intertidal species association has to be regarded as an intertidal extension of a typically subtidal species association. Summer–winter comparison revealed a decrease in density and biomass within the high intertidal species association.

Acknowledgments

The first author is funded by the I. W. T., Flemish Government. The research costs were supported by Marine Biology Section of the University of Ghent. The Department of Waterways and Coast provided information on the physical environment of the beach of De Panne. The authors are grateful to A. Soares, A. De Ruyck, and P. Meire for their valuable critical remarks on the manuscript. Several individuals assisted in the field and laboratory, including J. Van De Velde, M. Beghyn, D. Van Gansbeke, D. Schram, and A. Van Kenhove. Thanks to comments provided by two anonymous referees, the paper has been improved significantly.

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Received for consideration, September 1, 1998
Accepted for publication, January 5, 1999